AMERICAN MUSEUM NOVITATES

Number 677 Published by THE AMERICAN MUSEUM OF NATURAL HISTORY New York City Dec. 2, 1933

59.9, 53 P: 14.71, 58

THE SPERMACETI ORGAN AND NASAL PASSAGES OF THE SPERM WHALE (*PHYSETER CATODON*) AND OTHER ODONTOCETES

BY H. C. RAVEN AND WILLIAM K. GREGORY

INTRODUCTION

On the thirteenth of March 1928, a young male sperm whale, *Physeter catodon*, measuring eighteen feet three and one-half inches in length to the notch of the flukes, strayed into New York harbor. It was captured by longshoremen who towed it into the Gowanus Canal of Brooklyn, where it soon died. It is interesting to note that another young sperm whale sixteen feet long was taken in Vineyard Sound, about fifteen miles from New Bedford on the twenty-ninth of March 1842 (Jackson, 1847). The specimen taken in New York harbor was purchased from its captors by The American Museum of Natural History and brought entire on a motor truck to the museum. It was then my privilege (H. C. Raven) to dissect and study this extremely interesting animal. Of special importance were the highly specialized and hitherto little explored nasal passages and the spermaceti organ that is intimately related to them.

Pouchet and Beauregard (1885), Benham (1901), and Kernan and Schulte (1918), the able anatomists who have described the spermaceti organ and nasal passages of either *Physeter* or *Kogia*, have left us a bewildering mass of details with but indefinite clues as to the functions, origin or evolution of the several parts. It was only after repeated comparisons of the precise description by Kernan and Schulte of the anatomy of the nasal organs of a foetal *Kogia*, with the conditions recorded by one of us (H. C. Raven) in the young *Physeter*, that we began to be able to identify with any degree of confidence the probable homologies of the several parts in these two genera and were finally able to compare them effectively with the less specialized conditions in other odontocetes. In the present paper, we shall begin, therefore, with a brief summary of what has already been shown, by Abel and others, as to the origin and evolution of the highly peculiar nasal organs of the lower odontocetes; then we shall pass to a very brief description of the spermaceti organ, the spiracular sacs, and nasal passages of our specimen, stressing the

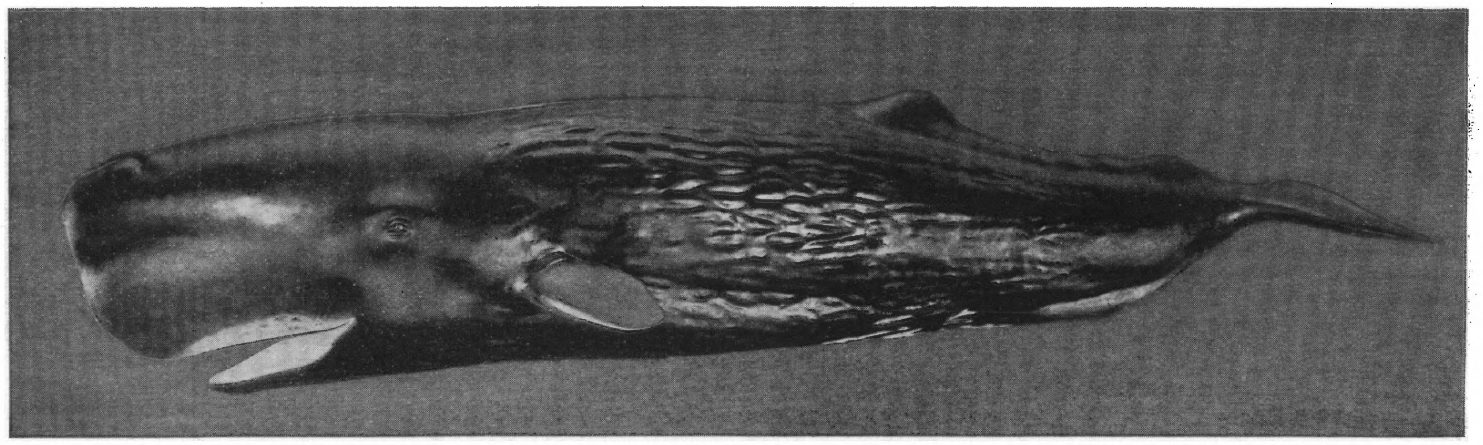

Fig. 1. *Physeter catodon.* Photograph of model of young specimen described in text.

evolutional and functional aspects of the parts noted in the dissection. This will lead first to an attempt to identify and equate the homologous parts in *Physeter* and *Kogia*, in the form of a convenient tabular summary, and finally to a discussion of the phylogenetic relationships of these two genera with each other and with the known fossil physeteroid genera of Miocene times.

EVOLUTION OF THE NASAL REGION IN ODONTOCETES

Probably whalers have seldom, if ever, suspected that all that part of the huge bow-like head of the sperm whale that contains the "case" and its precious contents—the spermaceti oil—is nothing more nor less than a titanic nose, the greatest nose on record. Nor have anatomists deigned to use such a simple concept in their highly technical descriptions. However, thanks to the illuminating works of Abel (1902) and Kellogg (1928), we can now view the anatomy of the nasal region of the sperm whales in the light of the general evolutionary history of the order as a whole. To begin with, we are met with the objections of Gidley (1913) and Miller (1923) that the archaeocetes of the Eocene and Lower Oligocene were not ancestral whales. While this is doubtless true of the excessively specialized *Zeuglodon* and its near relatives, yet the skull of *Protocetus atavus* Fraas (1904), of the Lower Oligocene, although perhaps too late in time, points the way unmistakably toward the curious relations of the bones of the snout in both orders of whales.

Miller (1923) attributes the backward growth and displacement of the premaxillae and maxillae of odontocetes upon the top of the head to a kind of "telescoping" or sliding movement due to the pressure of the water upon the forwardly moving head, but it seems to us much nearer to the facts to associate it with the backward displacement of the nose (Figs. 2, 3) and the progressive acceleration and increase of this organ in earlier and earlier foetal stages. Indeed, Abel (1902) has very clearly shown that, as the upper jaw grew forward into a fish-catching rostrum (a type of muzzle that again and again has been evolved in marine vertebrates), the nose retreated to the top of the head, forcing back, as it were, the nasal bones, but supported beneath by the backwardly growing flanges of the premaxillae and maxillae which finally reached to the occipital crest. Meanwhile, doubtless in connection with progressively deeper diving habits, while the nasal cavities became hypertrophied into two or more distensible sacs, the nasal muscles that close and open the nostrils became greatly enlarged. Asymmetries also were developing, accompanied perhaps by regional and functional differentiations, so that

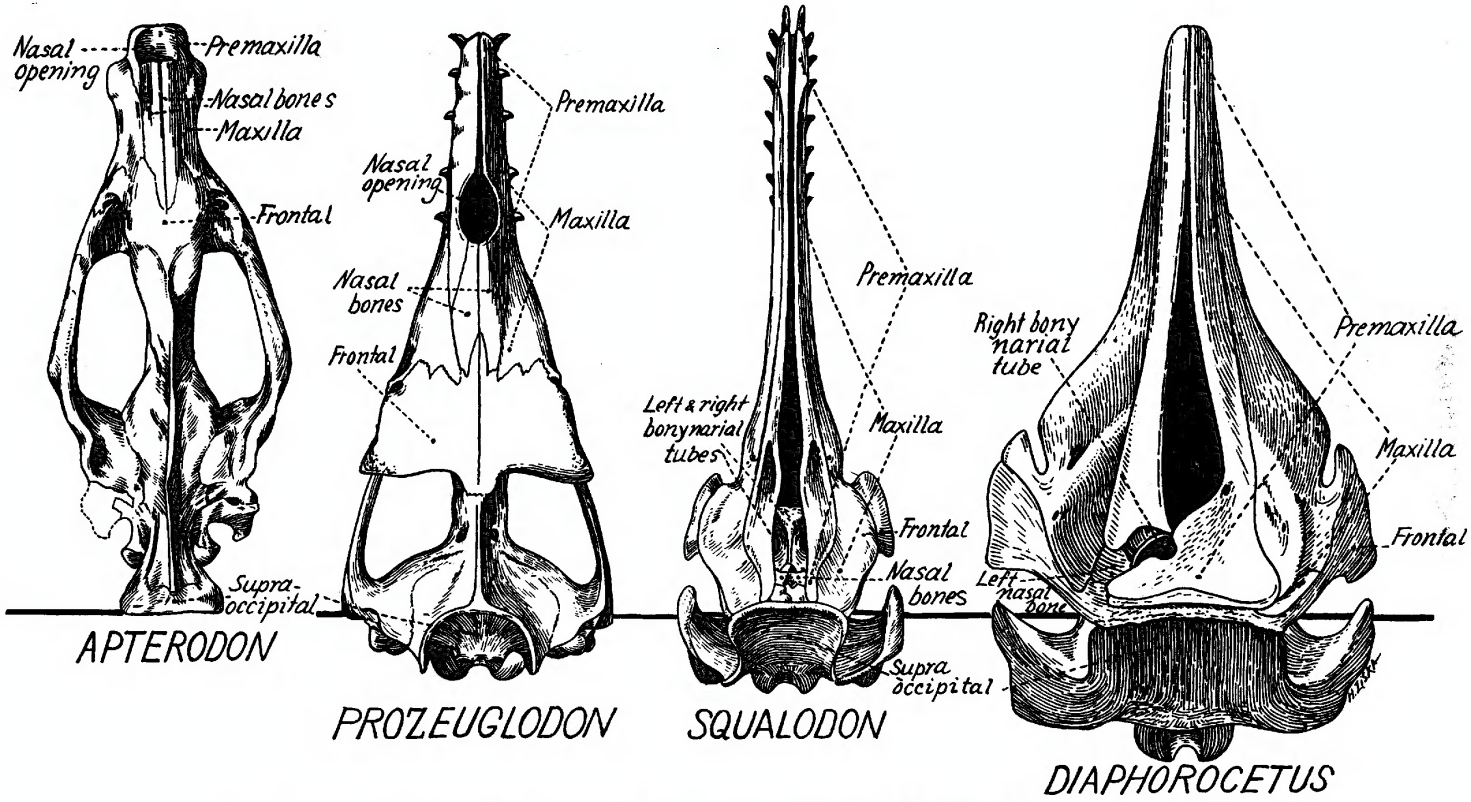

Fig. 2. Retreat of the nostrils and correlated specializations of the rostrum and skull-top in odontocetes.

All figures reduced to uniform length from premaxillary tip to occipital crest.

Semi-aquatic hyaenodont, *Apterodon*, Lower Oligocene, Fayûm, Egypt. After Osborn.
Primitive archaeocete, *Prozeuglodon atrox*, Lower Middle Eocene, Fayûm, Egypt. After Fraas.
Squalodon calvertensis, Middle Miocene, Maryland. After Kellogg.
Diaphorocetus poucheti, Lower Miocene, Patagonia. After Kellogg.

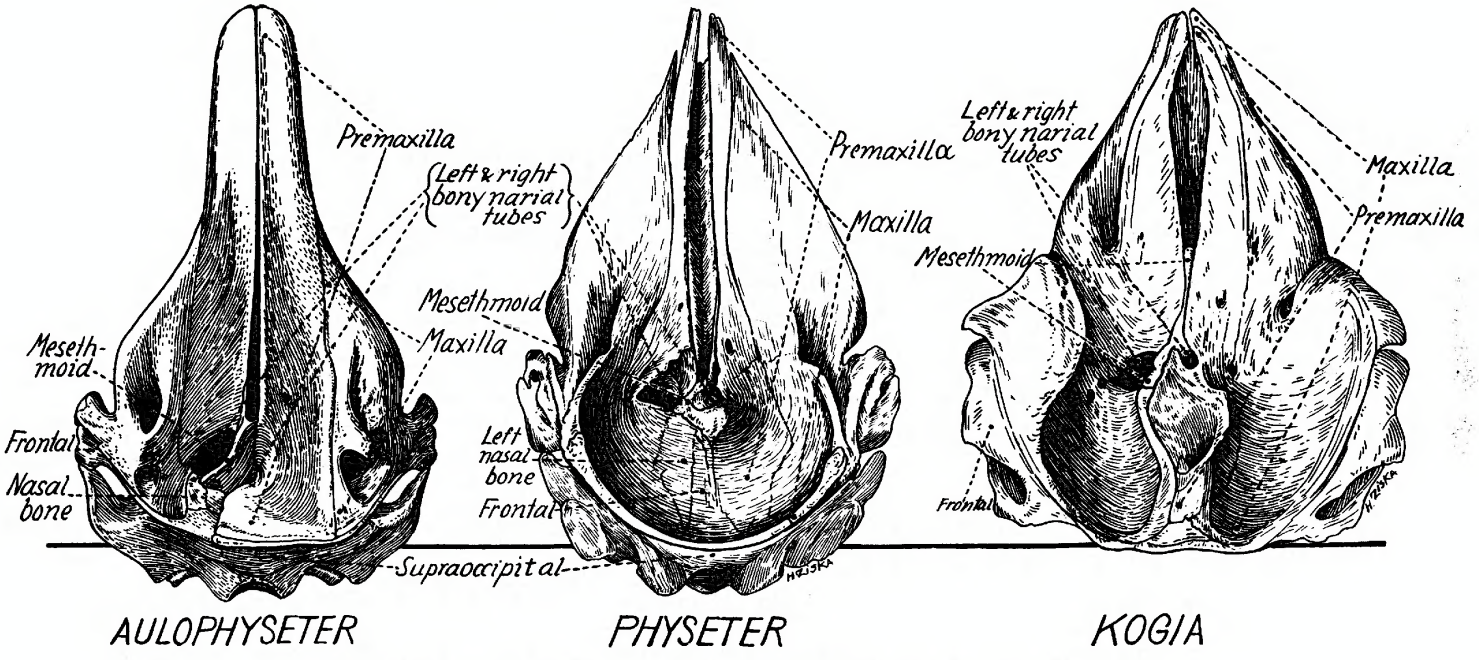

Fig. 3. *Aulophyseter morricei*, Middle Miocene, California. After Kellogg.
Physeter catodon. Skull of young specimen described in text.
Kogia breviceps. Skull of young specimen described by Schulte.

finally (in *Kogia*) the left bony narial tube (Fig. 3) became several times larger than the right, while in *Physeter* the right respiratory sac greatly predominated over the left (Fig. 4). The marks of these changes in the soft parts are impressed upon the bones that support them, so that we can very plainly see that even in *Diaphorocetus poucheti* (Fig. 2) of the Lower Miocene of Patagonia, which Kellogg figures as an early member of the sperm whale group, the great nasal turret, enclosed in a huge capsule of nasal muscles and stream-lined by surrounding adipose tissue, was already in existence. But, it may be noted at this point, this great nose was never a smelling organ, the olfactory parts of the skull having long since become atrophied. It was rather a gigantic organ for the forceful exhalation and inhalation of air, after and before long periods of submergence under high pressure.

EVOLUTION OF THE SPERMACETI ORGAN

We regard the spermaceti organ as merely a specialized central portion of the nose, reaching its highest development in the sperm whales but plainly foreshadowed in other odontocetes. In *Physeter* (Figs. 4–6) it is a sac-like mass of areolar tissue usually filled with oil and enclosed in a tough, muscular, fibrous sheath, occupying almost the entire upper part of the rostrum beneath the skin. We infer that its main function is to act as a force-pump for the bony narial passages, drawing a great quantity of air into the respiratory sacs and perhaps preventing the escape of air under the pressures of great depths. It may possibly also act in part as a hydrostatic organ, since by severe contractions of part of its muscular sheath the contained oil might be squeezed toward one end or the other, while the air sacs were being inflated, thus lightening the specific gravity of that end and tending to alter the direction of motion of the animal.

The beginning or at least a relatively early stage in the evolution of a spermaceti organ may, we conclude, be seen in other odontocetes, such as the narwhal (Fig. 7). In the American Museum Greenland Expedition of 1926, one of us (H. C. Raven) obtained an adult narwhal and made serial parasagittal sections of the frozen head. Figure 7 shows, above the bony rostrum, a mass of muscular, connective and fatty tissue enclosed in a muscular fibrous sheath that represents an early stage of the case of the sperm whale. Beneath the thick fibrous skin, this case is enwrapped with powerful nasal muscles, both transverse and oblique. The contraction of some of these would force the back part of the case into the left and right bony narial tubes and close the spiracular sacs and

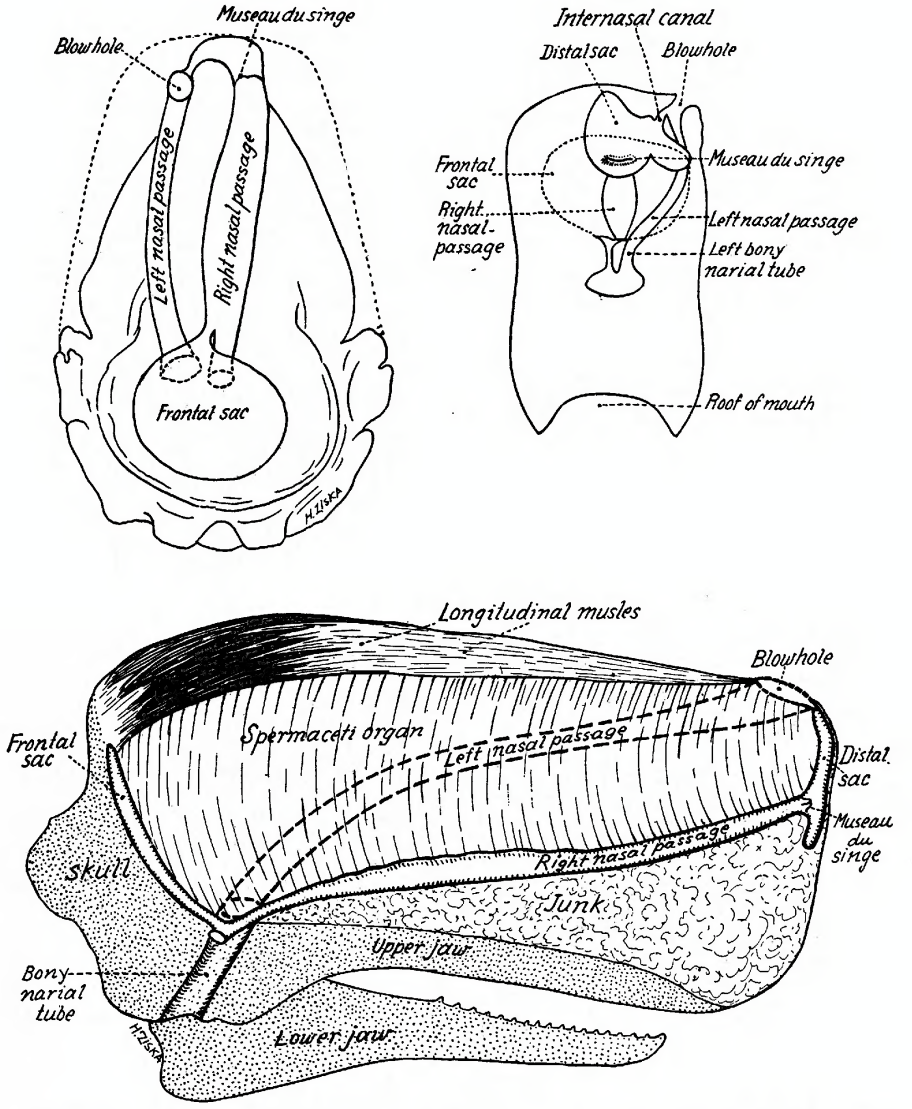

Fig. 4. Diagrams showing relations of the spermaceti organ to the junk and to the nasal passages in the young *Physeter*.

Top view; oblique view of head from right side; transverse section.

naso-pharynx. Hence we suspect that the primary function of the case is to make diving possible by firmly closing the outer and inner nasal passages. The large plug that fits into the left bony narial tunnel and the small plug that fits into the right narial tunnel are represented in the sperm whales by similar structures attached to the hinder end of the spermaceti organ. The latter (Figs. 5, 6) is a more or less unevenly ovoid sac with a tough wall of fibro-muscular tissue fastened below to a median raphe and resting on the "junk" or adipose cushion. The latter

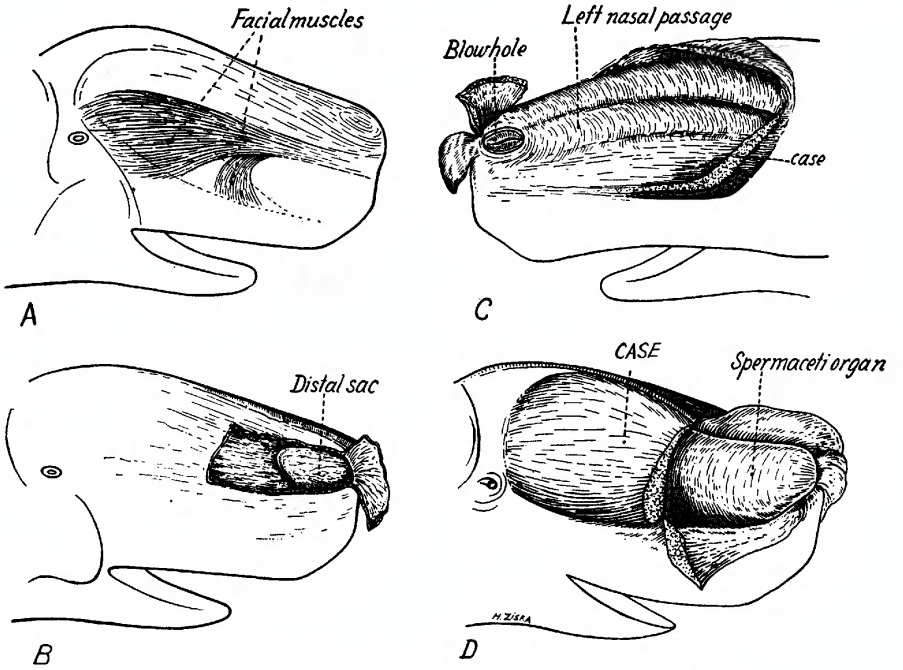

Fig. 5. Dissections of the nasal region of young sperm whale.

A.—After removal of blubber, showing superficial facial muscles.
B.—Distal end, right side, showing distal sac overlying spermaceti organ.
C.—Left side, case partly removed, showing blowhole and left nasal passage beneath transverse muscles of spermaceti organ.
D.—Right side, case partly reflected, showing spermaceti organ.

appears to be derived from the ventral portion of the muscular sheath that envelops the spermaceti organ. In *Kogia*, according to Kernan and Schulte's dissections (Fig. 8C), the junk appears to be represented by the median longitudinal muscle bundles, lying above the median rostral cartilage, which are connected posteriorly with the front walls of the air passages. In *Physeter* (Fig. 4) the junk consists of alternating vertical stripes of fibrous and fatty tissue. The junk in *Physeter* thus ties

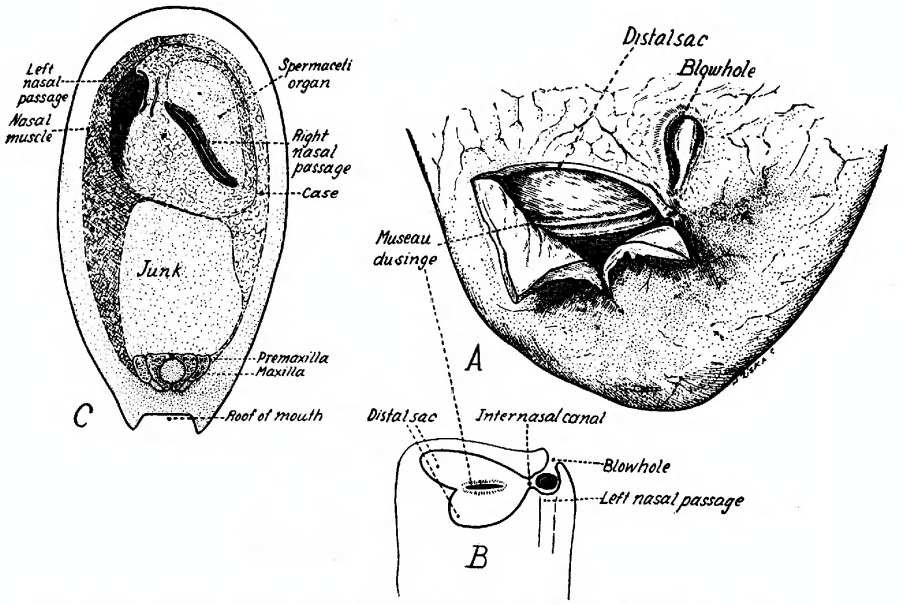

Fig. 6. Relations of the distal sac and associated parts in *Physeter*.

A.—Oblique dorsolateral view of front end of head, showing MUSEAU DU SINGE (right nostril) opening into distal sac.

B.—Diagram, front view, showing location of distal sac in young sperm whale, with MUSEAU DU SINGE opening into it from right nasal passage; blowhole opening into vestibule; internasal canal.

C.—Cross-section of front of head behind blowhole, seen from the rear.

A, C, after Pouchet and Beauregard.

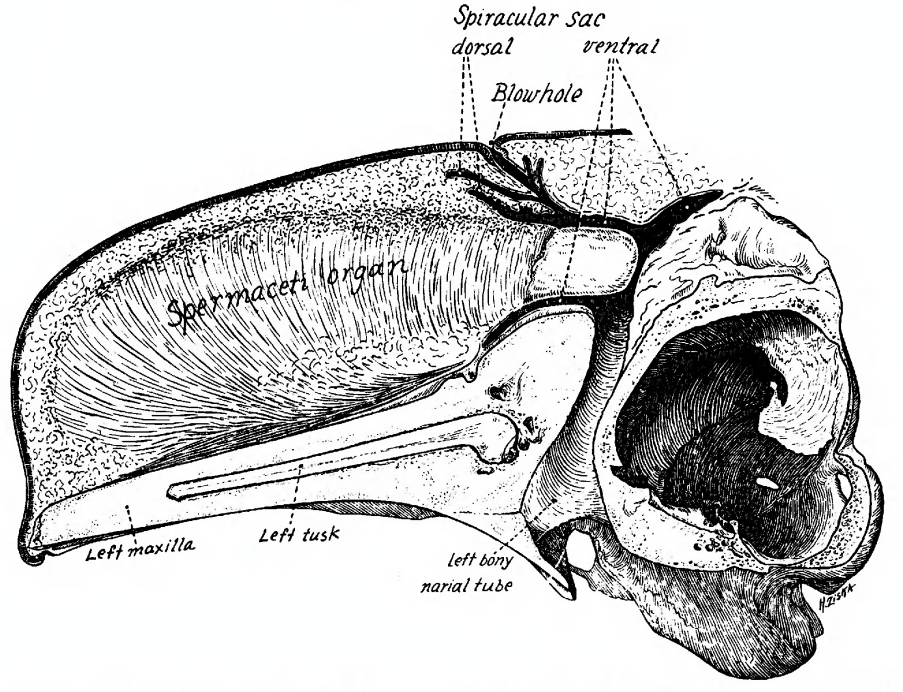

Fig. 7. Longitudinal section of the rostrum and skull of female narwhal (*Monodon*).

the movable spermaceti organ at its median base to the powerful bony rostrum.

The interior of the spermaceti organ, as is well known, contains an immense quantity (reaching as much as fifteen barrels) of the spermaceti oil. This cavity doubtless represents the concrescence of the numerous small spaces filled with oil that are to be found in the interior of the snout of ordinary toothed whales. Whatever other physiological functions the spermaceti organ may have, we are convinced that, with

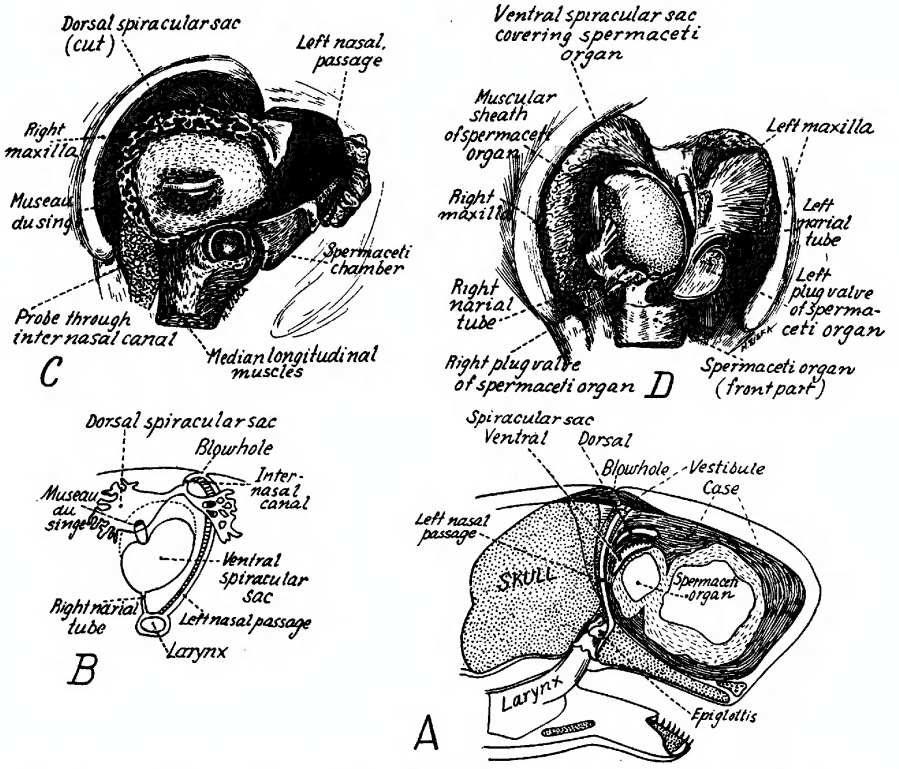

Fig. 8. A.—Diagram, longitudinal section of head of *Kogia*. After Benham.
B.—Diagram, front view, relations of spiracular sacs, etc., projected on transverse plane. After Benham.
C.—Foetal *Kogia*. Dissection of head, seen from above, after removal of blowhole and top of dorsal spiracular sac. After Kernan and Schulte. but with modified terminology.
D.—Foetal *Kogia*. Deep dissection, after removal of dorsal spiracular sac and upper part of ventral spiracular sac.
The floor of the ventral spiracular sac covers the rear part of the spermaceti organ. After Kernan and Schulte.

regard to the narial passages, one of its functions is to transmit the pressure from the muscles to the plugs or valves that project from its hinder end into the nasal passages. Although the more precise movements of these muscles and valves are, of course, difficult to discover, a contraction of the longitudinal muscles would protract the narial plugs of the spermaceti organ, thus opening the passage between the blowhole and the bony narial tubes, while contraction of the superficial musculature extending from the occiput forward would compress the spermaceti organ and close the entire passage.

THE SPIRACULAR SACS AND NASAL PASSAGES OF *PHYSETER*

We come next to the strange complex conformation of the "spiracular sacs" and nasal passages in *Physeter* which Pouchet and Beauregard mistook for dilatations of the spermaceti chamber (Kernan and Schulte, p. 245). *Physeter* is the only odontocete in which the blowhole (Fig. 9) is near the front end of the head; it also has perhaps one of the two most specialized of all known mammalian skulls (that of *Kogia* being the other) and its nasal passages reach the peak of regional differentiation and complexity. We may therefore conclude that the distal position of the blowhole in *Physeter* is a secondary or relatively recent specialization and that it is correlated with the enormous size of the spermaceti organ. Moreover, the distal position of the expansible spiracular sac, which will presently be described, may also have an appreciable effect in raising the front end of the long head when the animal wishes to rise from the depths.

The nasal passages of our young *Physeter*, which lie above the bony narial passages of the naso-pharynx, may now be briefly described. The blowhole lies on the surface of a boss that is located on the left side near the summit of the front end of the head (Fig. 9). The nasal slit (Fig. 5C), slightly sigmoid in shape and about eight inches long in our specimen, is guarded by subequal massive lips which are provided with sphincter and dilator muscles. The blowhole leads down into a small vestibule or dilatation of the left nasal passage (Fig. 6B). This vestibule is about five or six iches in diameter and seems to have been distensible. It is lined with smooth black epithelium and leads backward into the large pipe-like left nasal passage (Fig. 5C). This passage courses downward and backward just beneath the shell of nasal muscles surrounding the case (Fig. 6C) and just outside of, or lateral to, the spermaceti organ, past the plug-like valve that is attached to the spermaceti organ and down into the enlarged left bony narial tube. Thus the passage from the

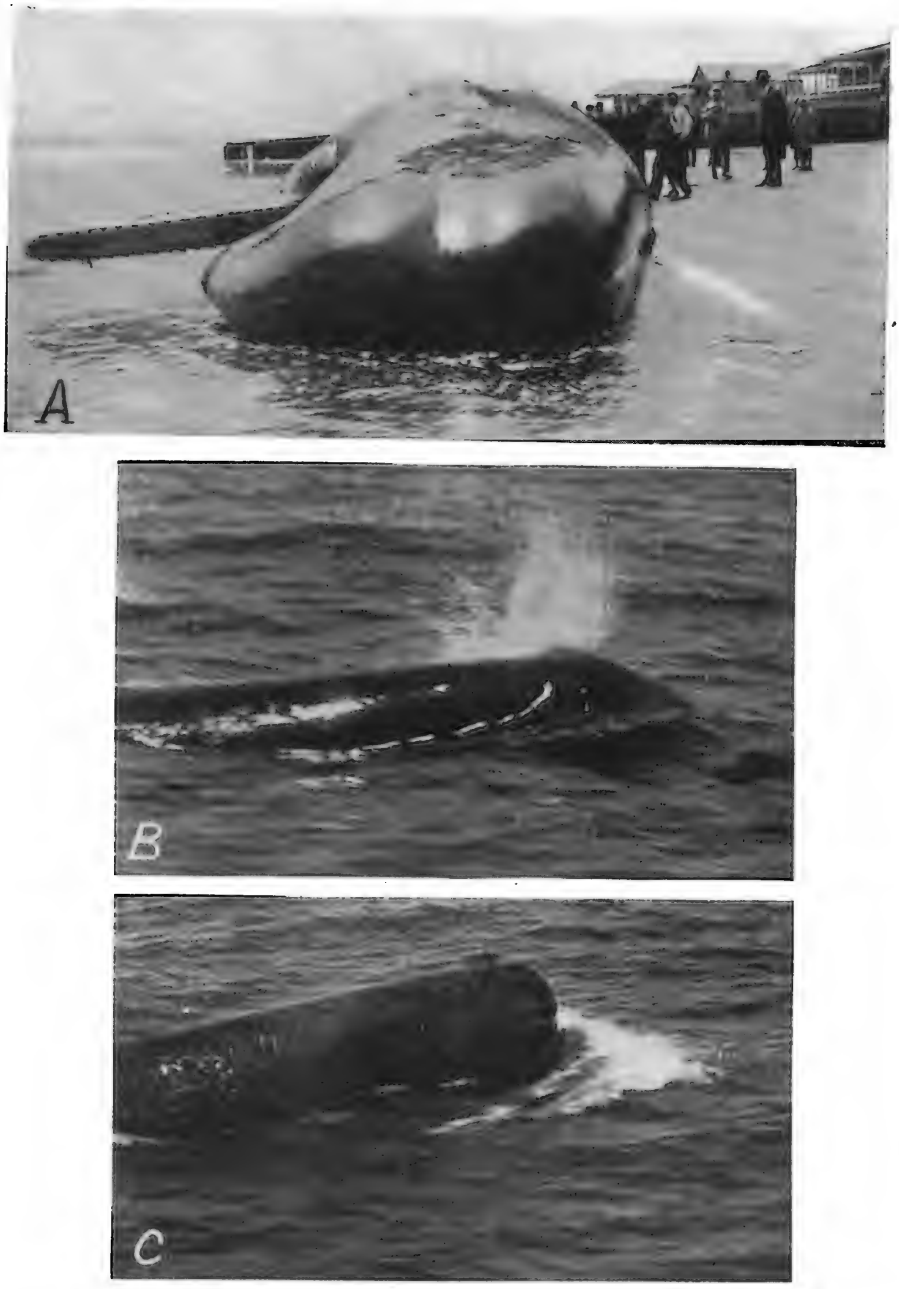

Fig. 9. A.—Front of head of adult sperm whale. The swellings indicate the position of the distal sac, at the right, and of the junk, at the left.
B.—Sperm whale, head rising, exhalation at its maximum.
C.—Sperm whale, head sinking, spiracle dilated for inhalation.
Courtsey of Dr. Robert Cushman Murphy.

windpipe to the left nostril (the blowhole) is very direct and is blocked only by the crescentic valve of the spermaceti organ and by the lips of the blowhole.

From the front end of the vestibule a small canal, hereafter called the internasal canal (Fig. 6B), leads forward to a great distal sac, the homologue of the "dorsal spiracular sac" of *Kogia* (Fig. 8) as described by Kernan and Schulte. This sac in *Physeter* (Fig. 5B) is found wrapped around the bow-like front end of the enormous spermaceti organ and immediately beneath the muscular sheath of the latter. It is therefore the first cavity encountered on piercing the thick skin around the upper front end of the head. Seen from in front (Fig. 6B), this distal sac is irregularly triangular. Its hinder wall is perforated by a wide, nearly transverse, mouth-like slit (Fig. 6A, B), called *museau de singe* by Pouchet and Beauregard. This valve, which may represent the right nostril, is shaped like upper and lower lips and opens forward. Behind the valve lies the right nasal passage (Fig. 4A, 6C), which, unlike the left passage, is widely expanded and lies deep, mostly beneath the spermaceti organ and above the adipose cushion or junk. At the hinder end of the right nasal passage (Fig. 4A, B) and immediately in front of the small right bony narial tube, the right nasal passage gives off an immense diverticulum, which we may call the FRONTAL SAC, since it lies on the surface of the dorsal basin of the skull. This frontal sac is wrapped around the hinder end of the melon-like spermaceti organ, of which it forms, indeed, the posterior or caudal wall. It is also the covering of both the right and left spermaceti plugs that occlude the bony narial tubes. This frontal sac is evidently homologous with the "ventral spiracular sac" of *Kogia* (Fig. 8) which likewise surrounds the hinder end of the spermaceti organ. In common with that organ the sac would be compressed by the contraction of the great frontal dome of nasal muscles which is fastened around the raised bony border of the occiput and along the sides of the maxilla (Fig. 8D).

We are of course unaware of the precise movements and functions of the parts of the nasal complex, but it seems not improbable that the spermaceti organ and the nasal tubes and pouches may in some way regulate the effects of variations in pressure according to depth. For example, contraction of the longitudinal muscles of the spermaceti organ by pulling open the "spermaceti plugs" might allow air to come up from the lungs into the nasal sacs and passages, and thus relieve some of the pressure on the lungs. Possibly the pressures in the deeper chambers are greater than in the more superficial ones into which they open.

Thus the left nasal passage may be most used in quick exhalation and inhalation, while the right passage with its small openings and expanded sacs may be used in gradual adjustments of pressures.

COMPARISON OF THE PARTS OF THE NASAL APPARATUS IN *PHYSETER, KOGIA*, AND THE LOWER ODONTOCETES

We seem now to be in a position to try to homologize the various parts of the nasal complex in typical odontocetes, *Physeter* and *Kogia*, as in the appended table.

PHYLOGENETIC RELATIONS OF *PHYSETER* AND *KOGIA*

From inspection of the table, p. 18, it will be seen that we regard *Kogia* as essentially a dwarfed sperm whale, excessively specialized in its nasal structures but closely related to *Physeter*. We base this conclusion partly on the above comparisons of the soft parts, partly on the comparative osteology of the skull. The spiracular sacs, nasal passages and spermaceti organ of *Kogia* are only with difficulty compared with those of ordinary odontocetes but are readily interpretable as a specialization beyond the stage illustrated in *Physeter*.

This interpretation is supported by the fact that in its skull, *Kogia* represents the extreme stage (Fig. 3) in a process of brachycephalization. If we express the maximum skull width, across the top of the orbits, as a percentage of the basilar length, from premaxillae to occipital condyles, we obtain the following series:

Prozeuglodon	*Squalodon*	*Diaphorocetus*	*Physeter* (Young)	*Kogia*
35	31	52	60	91

Doubtless this is not a direct phylogenetic series but it sufficiently well illustrates the extreme widening of the cranium and secondary abbreviation of the rostrum in the end forms, a process that has taken place to a lesser degree in other series of odontocetes, especially in the lines leading to *Orca*, *Monodon* and the Ziphiidae.

Second, the dentition of *Kogia* is highly specialized: (a) the maxillary teeth are reduced to one or two pairs in the adult (Schulte 1917, page 377); (b) these teeth are set in a continuous alveolar groove; (c) the symphysis of the mandible is secondarily abbreviated, a long symphysis with a high number of mandibular teeth being conspicuous in the numerous, less specialized Miocene odontocetes (Kellogg, 1928, pp. 176, 177).

Third, the disparity of the left over the right bony narial tube is even more pronounced in *Kogia* than in *Physeter*.

Fourth, the same extreme disparity and asymmetry in *Kogia* is noticeable in the bony fossae borne on the dorsal surfaces of the backwardly extended premaxillae and maxillae; these severally support the enlarged right ventral spiracular sac and the curving spermaceti organ which is pushed into it. Kernan and Schulte compare this part of the spermaceti organ to a finger crooked toward the right; as a result of the extreme backward displacement of the spermaceti organ, the ethmoid septum is sharply deflected toward the left. The left maxilla bears a "sagittal" crest marking the limits of the spermaceti organ, while all trace of the left nasal bones has disappeared. In *Physeter*, on the contrary, the huge spermaceti organ is extended far forward on the less reduced rostrum. The frontal sac also has become so huge that it has pushed the enclosing sheath of nasal muscles up on to the narrow rim of the occipital crest (Fig. 3).

It is possible that these differences between *Kogia* and *Physeter* may measure the amount of divergence from a relatively late stem form, such as the Middle Miocene *Aulophyseter morricei* (Fig. 3) as figured by Kellogg (1928, Figure 14), in which evidently neither the spermaceti organ nor the frontal sac had attained the huge development seen in *Physeter*. At any rate we suspect that the anatomical and osteological differences between *Kogia* and *Physeter* are of less than family value. This seems to be in harmony with the following passages from Schulte (1917, pp. 401, 402):

". . . It has not seemed desirable to retail the profound resemblances which have served to collocate the two forms since the first observation of the skull of *Kogia*. As compared with one another *Kogia* seems to show more striking modifications of the cranium, in only a few characters does *Physeter* possess equally marked peculiarities. . . .

After further discussion of the divergent differences, Schulte continues:

"The conclusion seems therefore warranted, subject to the limitation that cranial characters are alone considered here, that *Kogia* is the more highly modified form but that both have deviated in different directions from the common ancestral type."

SUMMARY AND CONCLUSIONS

1.—The SPERMACETI ORGAN is a mass of fat-filled areolar tissue which has arisen as a specialization of the deep parts of the nose, pari passu with the retreat of the nostrils to the top of the skull and with the formation of a nasal turret, consisting of respiratory sacs surrounded by nasal muscles. The hinder or caudal end of the spermaceti organ lies between the left and right nasal passages, which are occluded by fleshy plugs that project from its hinder end.

2.—In *Physeter* the spermaceti organ extends the whole length of the rostrum in front of the FRONTAL SAC; the latter is a diverticulum from the right nasal passage and closely surrounds the rear end of the spermaceti organ.

3.—In *Physeter* the DISTAL SAC, which is an expansion of the right nostril cavity, leads back through the MUSEAU DE SINGE or right nostril into a long, greatly expanded right nasal passage which lies beneath the huge spermaceti organ. In *Kogia* the right nasal passage is very short and is surrounded by the winding pillar of the spermaceti organ; the distal sac (called the "dorsal spiracular sac") is greatly expanded but with the extreme shortening of the snout now lies above the eyes, as does also the blowhole.

4.—In *Physeter* the spermaceti organ and its surrounding muscular sheath, besides assisting in the closure of the nasal passages after inhalation, may also function in other ways: (*a*) opening the spiracular sacs, (*b*) admitting small quantities of air under high pressure from the lungs to the distensible right nasal passage and frontal sac, (*c*) possibly also in shifting the center of gravity of the snout by suitable movements of the air, oil and blood contained in the several reservoirs.

5.—While in general *Kogia* is more highly specialized both in the soft parts and in the skeletal supports of the nasal complex, both genera seem to be derivable, at least in this region, from some of the Mid-Tertiary physeteroids, especially *Aulophyseter morricei* as figured by Kellogg.

6.—The "telescoping" of the maxillae and premaxillae on to the top of the skull in odontocetes seems to be attributable rather to the backward shifting of the nasal turret than to the direct push of the water upon the forwardly moving rostrum.

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Primitive Cetaceans *Protocetus* (Fraas)	Typical Odontocetes *Tursiops, Neomeris* (Brazier Howell) *Monodon* (H. C. Raven)	Sperm Whales *Physeter* (H. C. Raven)	Sperm Whales *Kogia* (Kernan and Schulte)
Nostrils symmetrical above middle of long rostrum	Nostrils retracted to above orbits, asymmetrical, the left (=blowhole) enlarged	Blowhole removed to near distal end of rostrum	Rostrum greatly shortened, blowhole above orbits
		Vestibule, immediately below blowhole	"Vestibule" (Fig. 8A)
		Internasal canal (connecting right and left nasal passages)	"Canal connecting vestibule and dorsal spiracular chamber" (Fig. 8C, probe)
Nostrils enclosing small cavities	Cavity of nostrils expanded, giving rise to 2 or 3 respiratory sacs	Distal sac, containing museau du singe (=right nostril) (Figs. 4, 5, 6)	"Dorsal spiracular sac" containing "orifice of right passage" at bottom
		Left nasal passage (Fig. 6C)	"Left nasal passage" (Fig. 8B)
		Right nasal passage, elongate and greatly expanded, beneath spermaceti organ (Figs. 4, 6)	"Right nasal passage," greatly shortened
		Frontal sac, behind spermaceti organ (Fig. 4)	"Ventral spiracular sac" folded around spermaceti organ (Fig. 8)
Nasal muscles enclosing cavities of nostrils and mucous tissue	"Melon" of fat-bearing tissue enclosed in sheath of facial muscles (Fig. 7)	Spermaceti organ long, containing huge oil chamber	Spermaceti organ short and high with voluminous oil chamber (Fig. 8A)
	Left narial plug, hinder end of melon	Left narial plug attached to spermaceti organ	"Rostral wall of left air passage" (Fig. 8D)
	Right narial plug, hinder end of melon	Right narial plug attached to spermaceti organ	"Caudal pillar of spermaceti organ"